

# Resource quality and trophic structure in the soil system

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## INTRODUCTION

'In seeking ways to reduce the apparent complexity of the ecosystem to a manageable level, ecologists have adopted, with varying success, a number of different (not mutually exclusive) bases for their work, such as the trophic level concept; the cyclic flow of carbon atoms; the community concept; the unidirectional flow of energy; the generalized Lotka-Volterra equation; and several others.' Platt & Denman (1978) thus introduced an analysis of the structure of pelagic marine ecosystems. Their comment is relevant to the discussion of trophic structure in the soil system because the diversity of microflora and fauna in soil, combined with practical problems of sampling and observation on relevant scales of time and space, have inhibited soil ecologists from developing a satisfying cohesive picture of the inter-relationships between soil organisms. Whilst we have considerable information on the composition of soil populations, and on the biology of individual species, we have not managed to combine this information with that of soil and ecosystem processes—the concluding point of Coleman, Reid & Cole (1983) in their constructive review of soil biology.

Coleman *et al.* (1983) also emphasize the need to examine the application to soil ecology of theoretical aspects of ecology developed from above-ground and aquatic research. Definition of trophic levels in the classical sense of Lindeman (1942) has proved particularly difficult to translate into the trophic structure of soil systems, the plant-herbivore-carnivore chain being confounded by recycling of production within the microflora. However, some recent emphasis on the importance of size as a basis for understanding feeding relationships in ecosystems (Platt & Denman 1978; Cousins 1980) could usefully be incorporated into soil biological research. Similarly, the ideas of life-history strategies based on the definitions of *r*- and *K*-types by MacArthur & Wilson (1967), with the addition of a second dimension of adversity (*A*) or stress (Southwood 1977; Grime 1979), has begun to clarify organism inter-relationships in soil (Greenslade 1982; Heal & Ineson 1984; Pugh 1980; Swift 1984).

There are many examples of conceptual trophic models which identify a sequence of transfers of carbon, energy or nutrients between organisms. These models attempt to classify the organisms functionally as saprophages and biophages or as biotrophs, necrotrophs, and saprotrophs or as herbivores, decomposers, microbivores and carnivores (see Swift, Heal & Anderson 1979). Such models have, however,

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proved inadequate to describe the functional organization of soil organisms quantitatively except at the broadest level of resolution. They lose the finer understanding of inter-relationships described in the earlier qualitative research founded on more detailed taxonomic analysis, especially amongst fauna, of specific habitats such as decomposing logs (see Elton 1966). The problem is partly practical, since different techniques are required for microbial and faunal research, and partly due to the flexibility of feeding relationships, in which there are recurrent cycles of microbe feeding on microbe, and of fauna ingesting and probably assimilating both plant and microbial material.

In this paper we will not go into the details of organism inter-relationships—these are dealt with in the individual papers of this volume. Nor do we attempt to provide an all-embracing definition of trophic structure: that is beyond our comprehension. Instead, we focus on:

- (i) the main basis of the trophic structure in soil (dead plant material) examining its variation in quality;
- (ii) how variation in the resource quality can influence the composition and inter-relationships of the organisms dependent upon it, combining the general niche model of Swift (1976) with the concept of *r*-, *K*- and *A*-strategies;
- (iii) identification of the particular physical constraints associated with soil, which in combination with the influence of resource quality, suggest the occurrence of size-related systems—microtrophic, mesotrophic and macro-trophic;
- (iv) examination of results from some intensive ecosystem studies as an initial test of the hypothesis of the co-existence of three trophic systems.

## RESOURCE QUALITY

Plant and animal detritus entering the soil represents the initial food resource\* on which the trophic structures are developed. Resource quality influences the type and rate of growth of the microflora, and hence the grazing fauna, as well as influencing palatability to the saprotrophic fauna. A suite of factors determine resource quality: the composition of carbon and energy-providing substrates, concentration of essential nutrients, the presence and concentration of modifying compounds such as polyphenols which can inhibit or stimulate resource utilization, and the physical arrangement of the resource (Swift, Heal & Anderson 1979).

### *Surface resource quality*

The components of resource quality may be broadly defined chemically but the influence of the suite of factors is most clearly seen through the comprehensive data

\*The term 'resource' is used for any identifiable piece of detritus. The term 'substrate' is not used because of its more specific use in biochemistry and microbiology for a chemically defined substance (Swift, Heal & Anderson 1979).

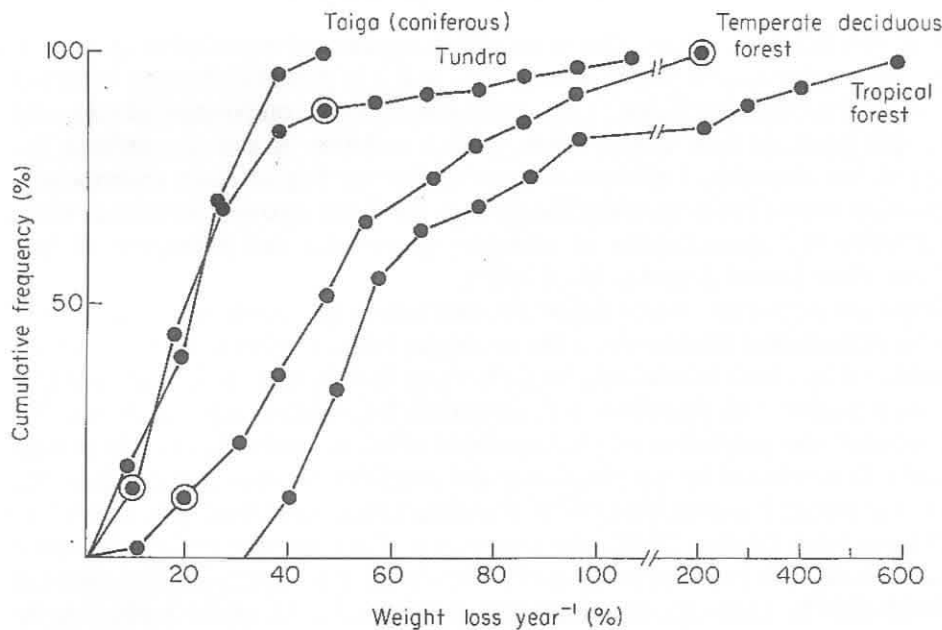


FIG. 1. Cumulative frequency curves of rates of litter and wood decomposition (% weight loss in first year) of a range of sites within a number of different biomes. In tundra and temperate deciduous woodland, minimum and maximum rates within a particular site (Moor House and Meathop Wood respectively) are encircled. Compiled from a wide range of literature.

now available on rates of litter decomposition (Fig. 1). The first year weight loss from litters integrates losses through catabolism, leaching and comminution, resulting from a combination of abiotic factors, microbial and faunal activity. The pattern is of a broad distinction between decomposition in different biomes through the influence of climate but with a wide variation within each biome reflecting mainly the variation in resource quality. The samples of resource types do not necessarily correspond to the actual proportions of different qualities within a biome; the selection has been determined by the various research workers, but in each case a wide range of species and plant parts are included. This is indicated by two examples in which the minimum and maximum values recorded within a site are shown, emphasizing the point that within a site there is a wide range of decay rates related to resource quality and that there is the opportunity for development of different trophic relationships.

#### *Below-ground resource quality*

Unfortunately, although there is a wealth of information for surface litter input from plants, we are still remarkably ignorant of both the quality and quantity of below-ground inputs and of their rates of decomposition. In a few studies concerned with root input and decomposition, the majority of work has been con-

cerned with live roots. Resorption of soluble inorganic and organic fractions probably occurs prior to root death, as in leaves, and it is probable that the observed rates of decomposition (Table 1) are overestimates of decomposition of naturally dead root litter. As with surface litters, there is variation in root composition, for example, the size-related nitrogen content and decay rate of *Pinus resinosa* and *P. sylvestris* roots (Table 1), while *Pseudotsuga menziesii* mycorrhizal roots contain about twice the concentration of nitrogen, phosphorus and potassium of fine (<5 mm diam.) roots (Fogel & Hunt 1983).

Root exudates may also be important elements in the below-ground contribution to decomposer communities; for example, Smith (1976) calculated annual exudation from three hardwoods, in kg ha<sup>-1</sup>, to include carbon 4, total nitrogen 0.8, total sulphur 1.9, phosphate 0.2, potassium 8.1, calcium 3.6 and sodium 34. The amount and proportion of photosynthate which is exuded from roots is very variable. It is affected by the plant's age and physiological state and a number of soil environmental factors. Up to 80% of translocated assimilate may be exuded as in *Pinus contorta* (Bowen 1980). The importance of this resource to the soil trophic structure is difficult to assess because of its variability and localization. As indicated by Smith (1976), exudates, containing simple carbohydrates, amino acids, organic acids and minerals, mediate the composition of the rhizoplane microflora with stimulation of gram-negative bacteria, spore germination, mycelial growth of pathogenic fungi and hatching of parasitic nematode eggs. The effects of changes in the amount, and possibly composition, of exudates to the composition of the rhizosphere microflora is shown by the low carbohydrate demand of mycorrhizal fungi from early successional stages of birch compared with the larger demand of species later in the succession (Dighton & Mason 1984).

The influence of the variety in quality and quantity of below-ground resource input on the trophic system may be (i) highly restricted to the rhizoplane and rhizosphere microflora and associated microfauna (Coleman *et al.* 1983), (ii) extended by mycorrhizal hyphae to beyond the rhizosphere with the possible development of a mesofaunal food link (Finlay, p. 319) or (iii) generally distributed in the soil through macrofaunal consumption of live or dead roots. Data on the effect of the quality of roots on macrofauna are limited but Lavelle, Sow & Schaefer (1980) showed that pulverized live roots of the grass *Loudetia simplex* supported less growth of young earthworms (*Millsonia anomala*) than comparable leaf material, corroborating the indications from the chemical and decomposition data that roots are of lower quality than above-ground parts. Growth was influenced by the state of decomposition of both leaf and root material and by the aerobic or anaerobic conditions for decomposition. Initial plant resources of high quality ensured an energy supply sufficient for both worms and microflora. With increasing humification resource quality declined leading to competition between worms and microflora for the available resources. When only complex plant residues remained, a symbiotic association between the microflora and earthworms was required to provide suitable enzyme suites to utilize the more recalcitrant resource. Although the interpretation by Lavelle *et al.* (1980) remains an

TABLE 1. Rates of weight loss of root litter: examples from published literature over a wide range of species and site conditions

Weight loss (% 1st year <sup>-1</sup> )	Diameter (mm)	Bag mesh size (mm)	Position in site	N (%)	Initial lignin (%)
1. <i>Pinus resinosa</i> : live roots					
11-16	0.5	0.4	{ Surface and 0-15 cm	1.0-1.3	22-25
15-24	0.5-3.0	0.4		0.6-0.8	22-23
25-48	0.5-3.0	3.0		0.6-0.8	22-23
2. <i>P. sylvestris</i> : live roots					
10-27	1-2 to 9-11	1	F+H	0.3-0.6	21-22
3. <i>Vaccinium vitis-idaea</i> : live rhizomes					
15 ± 0.9	1-2	1	F+H	0.5	31
4. <i>Calluna vulgaris</i> : live rhizomes					
5.3 ± 0.44	2-3	1	F+H	0.3-0.4	28
5. <i>C. vulgaris</i> : live rhizomes and below-ground stems					
5.0 ± 2.0	c. 2-3	1	0 cm	0.7	49
0.6 ± 0.3	c. 10	unconfined	0 cm	0.5	35
6. <i>Eriophorum vaginatum</i> : live roots					
8-19	c. 3	1	0-23 cm	0.5	34
7. <i>Juncus roemerianus</i> : live & dead (a) roots, (b) rhizomes					
(a) 17	—	—	5 cm	—	—
(b) 26	—	—	5 cm	—	—
8. <i>Spartina cynosuroides</i> : live & dead roots and rhizomes					
20	—	—	5 cm	—	—
9. <i>Larrea tridentata</i> : live roots					
0.21-0.45 day <sup>-1</sup> (over 38-141 day)	—	—	10 cm	—	—

Sources: 1, McClaugherty, Aber & Melillo (1982); 2-4, Berg (1984); 5&6, Heal, Latter & Howson (1978); 7&8, Hackney & de la Cruz (1980); 9, Comanor & Staffeldt (1978).

hypothesis, the emphasis is that the inter-relationship between fauna and microflora, is affected by resource quality (Lavelle 1983).

### INFLUENCE OF RESOURCE QUALITY ON TROPHIC STRUCTURE

There are many papers (see Dickinson & Pugh 1974) describing field variation in microbial and faunal populations associated with different resource and substrate types, decomposition of a particular type of litter, and laboratory experiments on the influence of different resources and substrates on growth or ingestion by microflora and fauna. Swift (1976) provided a general model which helps to clarify the basic resource characteristics which determine the diversity and composition of the microflora (Fig. 2a). He recognized that the variety of fundamental niches available in a resource entering the decomposer system was represented by its range of component substrates and by its physical structure. As the resource decomposes, the range of substrates is reduced as labile fractions are metabolized, but there is

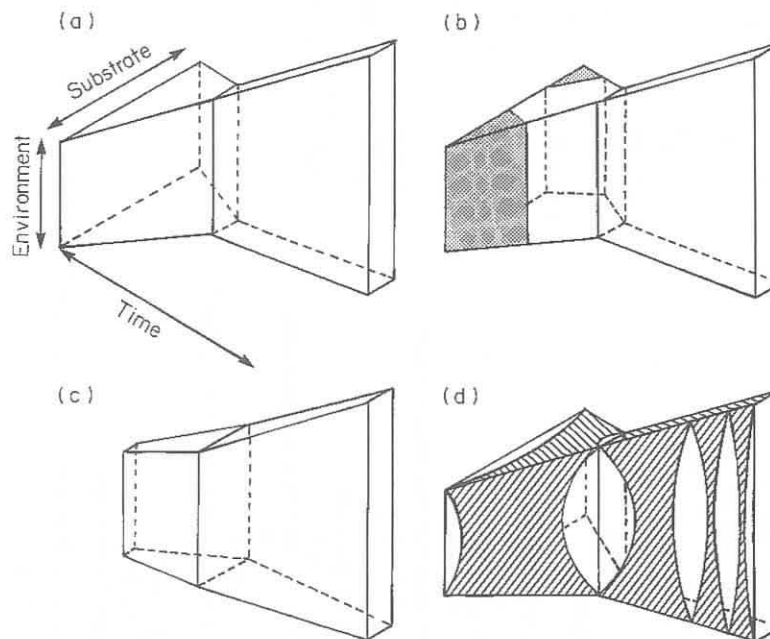


FIG. 2. Changes in the potential variety of fundamental microbial niches within primary resources of different quality during decomposition. A cross section of the volume at right angles to any point in time represents the available niche space in relation to the two major determinants, environment and resource. The time-scale is simplified to represent two stages in decomposition: the initial rapid exploitation phase characteristic of primary resources and the much slower interaction phase of the terminal resources (see text). (a) General model representing high resource quality (from Swift 1976). (b) Initial substrate availability masked by the presence of inhibitory chemicals, e.g. polyphenols. (c) Low quality resource, e.g. wood with a limited range of substrates. (d) Availability of niches limited by periods of severe climate, e.g. drought or cold.

some compensation through production of secondary substrates. The gradual physical disruption of the resource over time increases the physically determined niches available to organisms.

Swift's general model of niche availability during decomposition, may be modified by resource quality. For example, the presence of secondary compounds selected to inhibit leaf consumption by herbivores can inhibit the availability of substrates in an otherwise high quality resource (Fig 2b). A second variation is of a resource such as wood, in which substrate and physical availability is initially limited (Fig 2c). As decomposition proceeds, the range of niches expands with production of metabolites from lignin and cellulose decomposition and physical disintegration, the latter particularly associated with a phase of faunal colonization (Swift 1976). A third situation may be represented as in Fig 2d, in which severe climatic conditions such as cold or drought, restrict niche availability to a few 'windows' in time.

The general model developed by Swift (1976) critically identifies the quality of the resource as the primary factor which selects the composition and characteristics of the microflora. The recurrent provision of fresh resources for colonization and their residence time are readily related to the concepts of disturbance or durational stability inherent in the selection for species along the  $r$ - $K$  continuum of MacArthur & Wilson (1967). A second dimension of adversity or stress defined by Grime (1979) and Southwood (1977) as modifying the  $r$ - $K$  continuum can be equated with low resource quality and severe climatic conditions. The recognition of the general principles of durational stability and adversity has helped to explain patterns of fungal associations (Pugh 1980; Swift 1984) and has been extended to soil fauna (Greenslade 1982). However, it is essential to recognize that the selective effects of resource quality, representing degrees of durational stability and adversity, act not on single characteristics such as substrate utilization, but on a combination of morphological, physiological and phenological characteristics of the microflora. Given that resource quality influences the characteristics of the microflora populations, it is a logical consequence that it will influence the composition of the fauna which graze the microflora, as well as directly determining the composition of decomposer fauna. On this basis, Heal & Ineson (1984) hypothesized general patterns of development of microflora and fauna associations related to resource quality.

#### *High resource quality*

##### *Exploitation phase*

There is rapid colonization by microflora with small cell size or diffuse mycelium, and with maximum production and dispersal of propagules. Growth rates tend to be high on low molecular weight substrates, with high efficiency of conversion to biomass production. These colonizers tend to be demanding of nutrients as a result of their growth characteristics. Population growth is rapid and is often followed by a



sharp decline as readily available substrates are exhausted or as fauna exploit the food source. Fauna also tend to be small, with rapid growth rates and dormant dispersal stages, such as protozoa, or mobile and longer-lived, e.g. Collembola. Consumption by microfauna tends to disrupt populations, fragment and disperse the resource and enhance the rate of decomposition at an early stage. The exploitation phase, selecting organisms with  $r$  characteristics, merges into an interaction phase in which organisms tend to be of the  $K$  type.

#### *Interaction phase*

Associated with the more resistant substrates and slower decomposition, equivalent to greater durational stability, populations in the later stages tend to have large cell size or compact mycelium and slower growth rates than in the exploitation phase. With longer generation times interactions with competitors and grazers tend to be more stable, with development of defence mechanisms such as resistant cell walls and antibiotic production. Population dynamics tend to be damped, with more density-dependent control and faunal grazing is likely to be more selective. The increasingly resistant residue from decomposition selects for a limited range of specialized microflora, the characteristics of which are similar to the associations on low quality resources.

#### *Low resource quality*

Resources dominated by combinations of high molecular weight and resistant substrates, low nutrient concentrations and inhibitory compounds have slow decay rates and select for relatively specialized microflora with slow growth rates because of the intransigent substrates. Nutrient conservation mechanisms such as translocation help to overcome deficiencies and may be associated with large size. Microflora interactions are often intraspecific, reflecting the limited range of species present. Interactions between microflora and fauna may include intimate symbiosis in response to lower resource quality. Slow-growing microflora tend to develop physical or chemical defences against grazing, resulting in specific fauna-microflora relationships. Concentration of nutrients by microflora in nutrient-poor resources can gradually provide suitable food sources for fauna, e.g. in wood, and faunal colonization can enhance physical disintegration with exposure of new surfaces for exploitation (Fig 2c).

It is expected that the actual species involved in the succession of organisms on a particular resource type will be very variable; chance plays a large part in the initial colonization. The composition of populations adjacent to a new resource and current microclimatic conditions will influence the species succession. Sequences have also been obscured by the use of samples of resources rather than following the fate of individual resource units (Swift 1976). Thus, the populations of organisms developing on a resource do not follow a simple pattern. However, logic suggests that the diverse microflora and fauna of the soil is constituted from a



small-scale mosaic of resources which supports associations of organisms at varying states of development with distinctive inter-relationships. The characteristics of the organisms are constrained, however, by the physical environment of the soil, including that in the surface organic matter, as discussed in the next section.

#### PHYSICAL CONSTRAINTS ON TROPHIC RELATIONSHIPS

So far we have concentrated on the selection of species characteristics and population inter-relationships through variation in the quality of resource input both above- and below-ground. The feeding relationships are related to the size of the organisms, particularly amongst the fauna, which can be broadly grouped into micro-, meso- and macrofauna. As emphasized by Cousins (1980), fauna do not distinguish their prey on the basis of the past history of the prey, i.e. whether it is a herbivore, microbivore or carnivore; size is a much more important criterion. Platt & Denman (1978) suggest that the body weight of prey is typically from 0.01 to 0.1% of their predators. Within the soil, there are strong physical constraints on organism size, related to moisture characteristics, pore size and particle size. These constraints, when linked to resource quality, suggest that within the soil, three trophic systems may be recognized.

##### *Trophic systems*

###### *Microtrophic*

Largely confined within the water film in surface resources, on root surfaces and around soil particles, this is a system based on utilization by bacteria or yeasts of the more readily available carbon sources. Consumption of the microflora is by protozoa and nematodes, which may also be preyed on by protozoa and nematodes, still within the water film. The increase in weight from bacteria or yeasts to flagellates or small amoebae to predatory ciliates is probably of the order of  $10^{-15}$ – $10^{-13}$  to  $10^{-12}$ – $10^{-9}$  to  $10^{-9}$ – $10^{-7}$  g. The size of individual organisms will have increased considerably but only the larger ones have the capacity to break the surface of moisture films. The system is virtually contained within the moisture film, which will obviously be less inhibiting in moister habitats. Larger fauna are not commonly involved directly in this food web, although enchytraeids and some Diptera larvae may capitalize on concentrations of micro-organisms.

###### *Mesotrophic*

Largely confined to the air spaces within and between organic resources or to soil pores, this is a system based on the utilization by fungi of a wide range of substrates, including the less readily available carbon sources. The larger mass of mycelium and its extension into air spaces allows consumption by mesofauna, predominantly Collembola and mites, which have the capacity to move through, but

not significantly disrupt, the physical structure of the soil or litter. The physical size of spaces tends to limit the size of individuals and predation tends to be amongst the mesofauna. Some larger predators, such as pseudoscorpions and linyphiid spiders, may exploit this food web, particularly at the soil or litter surface, but individual body size or population density are not large enough to support macropredators. Size relationships are difficult to define because of the problem of identifying the individual fungus weight, but fungus-grazing Collembola and mites are of the order of  $10^{-7}$ – $10^{-4}$  g, with their predators at  $10^{-4}$ – $10^{-2}$  g.

#### *Macrotrophic*

With a body size or shape large enough to disrupt the physical structure of the soil or litter, macrofauna such as earthworms and millipedes transcend the physical limitations imposed on microtrophs and mesotrophs. They ingest both the basic resource and the associated populations of microflora and fauna. They utilize the concentrated nutrient and carbon sources of the high quality, initial resources or the concentration which has occurred through microbial decomposition or enhance concentration and availability through gut microflora. In each case, there is a large increment in body size, with the production of size units which can support larger predators, including vertebrates. Animals with large body size are unlikely to be supported directly from the microtrophic and mesotrophic systems because of the successive energy loss through the smaller size increments associated with the transfer along these more selective food webs.

It is recognized that the distinctions between these three trophic systems are blurred, but it is suggested that the physical limitations of the soil environment, combined with the varying quality of resources derived from the vegetation, results in a small-scale mosaic of trophic associations. These associations are not identifiable through the coarse sampling regimes adopted in most soil biological research, but are more recognizable when individual resource units can be isolated (Swift 1976) and the trophic relationships followed more directly. The dissipation of energy in the transfer of material along successive size-defined links in a food web may be a major limitation to the maximum size of organism that can be produced from small individual substrates, analogous to marine microtrophic associations (Pomeroy 1984).

### A CONVENTIONAL QUANTITATIVE APPROACH TO TROPHIC STRUCTURE

Although the complexity of the trophic relationships in soil systems has frustrated attempts to produce a satisfying synthesis of field data, it is worth re-examining the results of the intensive ecosystem research of the late 1960s and early 1970s to see to what extent the microtrophic, mesotrophic and macrotrophic systems are detectable, and are related to resource quality. The intensive soil fauna research at Moor House in the north Pennines was summarized by Coulson & Whittaker (1978), and

has been combined with microbial information from Collins, D'Sylva & Latter (1978), to provide a summary, however speculative, of the quantitative trophic relationships in one soil system (Fig 3).

In the acid blanket peat at Moor House, fauna are virtually confined to the

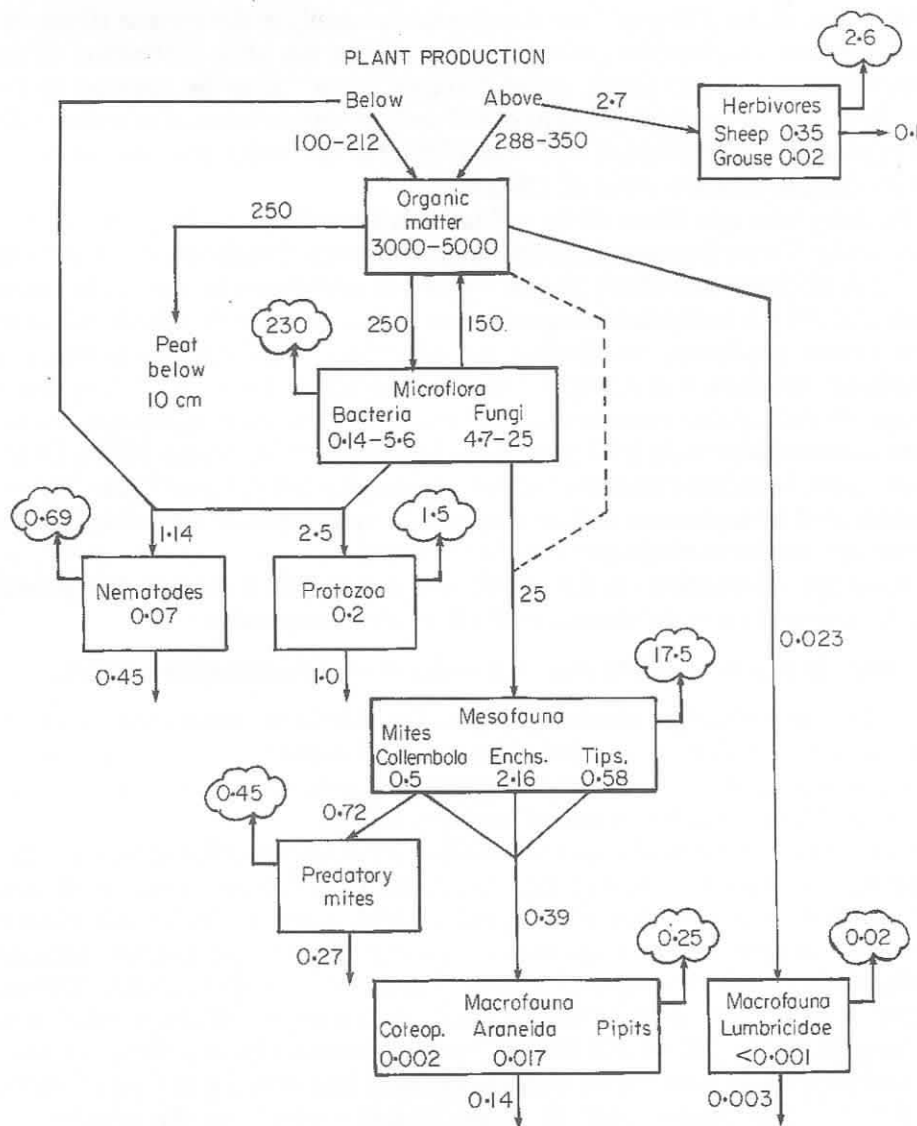


FIG. 3. A summary of the trophic structure of blanket peat (0-10 cm) at Moor House, Cumbria. Biomass in compartments is expressed as g m<sup>-2</sup> and transfers as g m<sup>-2</sup> year<sup>-1</sup>. Litter input, accumulated peat and transfer below 10 cm are based on Jones & Gore (1978). Bacterial and fungal biomass range represent dilution to direct counts and stained to total mycelium (Collins, D'Sylva & Latter 1978). Protozoa estimates, for testate amoebae only, are from Heal (1964). Other fauna data are from Coulson & Whittaker (1978).

surface 10 cm. The basis of the trophic structure is surface and root litter input of  $450\text{--}500\text{ g m}^{-2}\text{ year}^{-1}$  from *Calluna vulgaris*, *Eriophorum vaginatum* and *Sphagnum* spp. About half of the input passes into peat below 10 cm although the time taken may vary from 15 to 150 years depending on site conditions (Jones & Gore 1978). Thus, about  $250\text{ g m}^{-2}$  are decomposed annually in the surface 10 cm. No direct measure of microbial production is available, but after subtraction of the amount respired by the fauna, about  $230\text{ g m}^{-2}\text{ year}^{-1}$  must be respired by the microflora. Given a yield coefficient of 0.4 and the recirculation of microbial cells and hyphae produced (Heal & MacLean 1975), the best estimate of annual microbial production is of the order of  $150\text{ g m}^{-2}$ .

Defining who eats whom in the soil fauna is hazardous and the pathways indicated in Fig. 3 must be accepted as first approximations. Despite these reservations the results indicate that about  $25\text{ g m}^{-2}\text{ year}^{-1}$  is assimilated by the soil fauna, of which about 8 g is converted into production. If it is assumed that the fauna, apart from known predators, are feeding on microflora, then the microfauna and mesofauna assimilate 4 and  $25\text{ g m}^{-2}\text{ year}^{-1}$  respectively, i.e. 3 and 17% of microflora production. A few macrofauna (lumbricids) occur on the bog, but their assimilation is estimated at only  $0.02\text{ g m}^{-2}\text{ year}^{-1}$  (Coulson & Whittaker 1978). Of the  $8\text{ g m}^{-2}\text{ year}^{-1}$  produced from the 'microbivore trophic level',  $1\text{ g m}^{-2}\text{ year}^{-1}$  (12%) is assimilated by carnivores and, as emphasized by Coulson & Whittaker (1978), subsequent carnivore levels are severely restricted.

Although information on the microfauna is particularly limited, the general pattern seems to be of dominance of the food chain sequence:

organic matter  $\rightarrow$  microflora  $\rightarrow$  mesofauna  $\rightarrow$  mesofauna/macrofauna,

the major activity being recirculation within the microflora. In contrast, below the 10 cm level on the bog, near to the water table, metazoan and probably protozoan activity is negligible. Thus, the trophic system based on the slow decomposition of the residual organic matter is one of microflora alone.

Comparison of the blanket bog with adjacent soil systems at Moor House is also revealing. The transition from blanket bog, through *Juncus squarrosus* on shallow peat and *Nardus* grassland on alluvial peaty podzols and gleys, to *Agrostis-Festuca* grasslands on brown earth, represents a sequence of increased aeration, reduced acidity, higher quality of organic input and higher rate of organic matter turnover (Rawes & Heal 1978). Associated with this gradient is an increase in assimilation by the mesofauna (25, 56, 97 and  $69\text{ g m}^{-2}\text{ year}^{-1}$  respectively) and there is a more marked increase in macrofauna assimilation from less than  $1\text{ g m}^{-2}\text{ year}^{-1}$  in the blanket bog and *Juncus* peat to about  $73\text{ g m}^{-2}\text{ year}^{-1}$  in the *Nardus* and *Festuca-Agrostis* grassland with mineral soils (Coulson & Whittaker 1978).

Increased importance of larger organisms is associated with the increase in resource quality of the litters. This continuum may be seen in relation to the Swift model (Fig. 2), with the bog community providing a narrow substrate window and with waterlogging conditions restricting the environment parameter of the model. Increased soil fertility and reduction of environmental stresses in the grassland

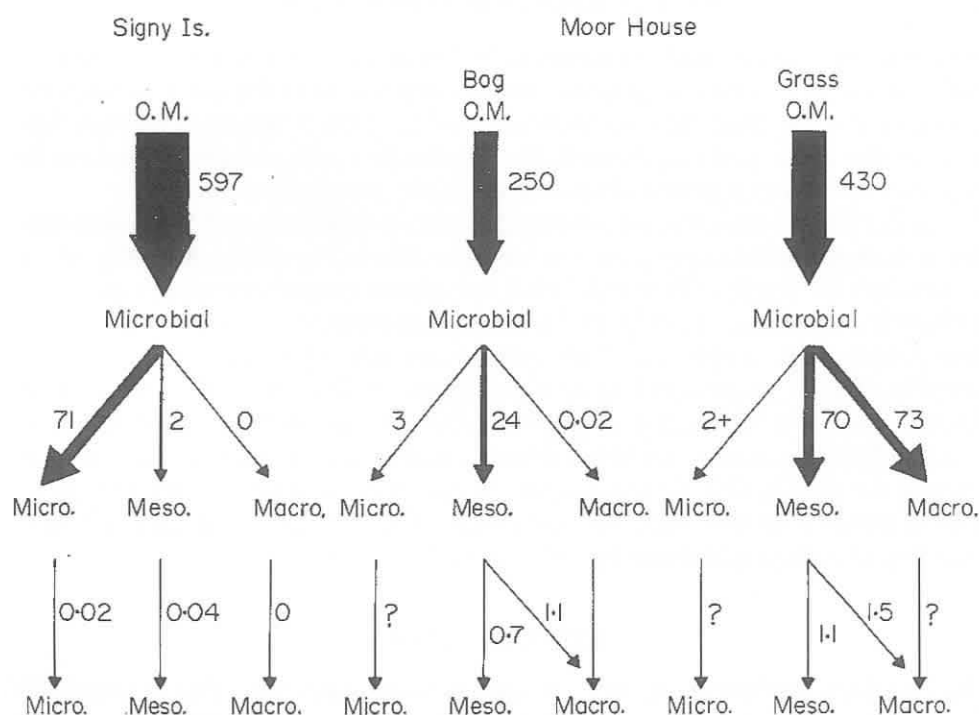


FIG. 4. The general trophic structure in the soil of three ecosystems, distinguished by variation in severity of climatic and resource quality constraints: (a) Signy Island moss bank in the Antarctic (from Davis 1980); (b) and (c) are respectively acid blanket bog and *Festuca-Agrostis* grassland on limestone, at Moor House in the north Pennines, UK (see text for details).

increase the initial resource quality window size. In the highly stressed blanket bog system, movement along the time axis decreases, rather than increases, decomposer niches on the substrate, hence residual organic matter tends to accumulate.

Quantitative information on the microfauna and microflora are limited but Fig. 4 shows a simplified summary of the trophic structure of the blanket bog compared with that of the adjacent grassland on which the nutrient constraint has been reduced. Also shown is the structure of an Antarctic moss community, an extremely simple community in terms of numbers of species, developed under severe climatic constraints (Davis 1980). The comparison of these three systems suggests differential expansion of distinct trophic structures related to variation in climate and resource quality.

The indications are that an increasing importance of fauna, and an increasing dominance of macrofauna, are related to improvements in the physico-chemical environment and in quality, rather than in quantity, of the residues of primary production. This interpretation from comparative descriptions tends to be confirmed by experiment, with particular emphasis on the nutrient quality of the plant material. Coulson & Butterfield (1978) showed that whilst the rates of decomposition of the same litters were similar on adjacent sites at Moor House, the contribu-

tion of fauna to decomposition tended to be larger on the mineral than on the peat soils. Fertilization with nitrogen increased the numbers of enchytraeids and tipulids on peats and increased the rate of decomposition through enhanced nutrient content of the plant material. Surprisingly, fertilization with phosphorus tended to reduce both rate of decomposition and soil fauna populations.

In this limited example, we see that the relative microflora and fauna contributions to decomposition processes are strongly affected by resource quality which determines the length of food chains and size of their component organisms. Cragg (1961) and Macfadyen (1963) synthesized and interpreted the limited data on soil fauna available for a few sites. Their general conclusions have been confirmed and amplified by the subsequent intensive studies on a wide range of sites (Petersen & Luxton 1982) but with a shift in emphasis. One of the conclusions of Petersen & Luxton (1982) was that 'chemical nutrient, rather than energy, availability may impose the most serious limitations on soil animal populations . . . more information is required on food substrate and space utilization before a complete understanding of niche exploitation by soil animals is attained'.

### CONCLUSION

Well defined, replicated patterns of species associations with clearly organized trophic structures are not expected to occur in soil systems. The diversity of resources and organisms, microbial flexibility and chance, mitigate against this. But neither is the composition of the microbial and faunal populations random. The argument developed in this paper is that the physico-chemical features of individual resource units select for distinctive combinations of morphological, physiological and phenological characteristics of the microflora. These in turn select for particular characteristics in the associated fauna.

Activities of the microflora and fauna modify resource quality with time, resulting in a change in the biota. Within any ecosystem, the wide variety in quality of resources entering the soil system results in a variety of microflora-fauna associations. The physical structure of the resources and of the soil superimposes additional constraints on the biota and differentiates three trophic systems which are broadly separated on size. The extent to which these micro-, meso- and macro-trophic systems are developed in any ecosystem is thus determined by the combined effects of resource quality and physical environment.

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